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Art. XIV.—*On the Geographical Distribution of the Sea-Grasses.*

A Preliminary Communication.

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Communicated by Professor A. J. Ewart.

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I.

For several years I have been studying the geographical distribution of the *Marine Flowering Plants*, as it seemed to me that it might have some general value both from a phylogenetic and a geological point of view.

We owe most of our knowledge on these plants to the late P. Ascherson, who, during a series of years, contributed to their study, and was much interested in their geographical distribution.

Some considerations will show why I think this phytogeographical study may be of more general interest.

The marine flowering plants—or *sea-grasses*—belong to two monocotyledonous families—viz., *Hydrocharitaceae* and *Potamogetonaceae*, both of which are included in the cohort *Helobieae*. This cohort consists of several families, nearly all of which are water-plants (or swamp-plants). They are very distinct from the other monocotyledons, and undoubtedly represent old types.

Sometimes it has been urged that from this cohort most of the other Monocotyledons and Dicotyledons have originated. Be that as it may, the Helobieae form an especially well-marked group within which the families show a progression from types with many free superior carpels to others with one syncarpous inferior ovary. In all the families, genera with one or a few species prevail, and within the whole cohort only one genus, *Potamogeton* (the Pondweed), is really rich in species. It seems as if, in most cases, the developing power of the genera has been checked.

The *sea-grasses* belong to—

(1.) 3 genera of *Hydrocharitaceae*—viz.: *Halophila*, *Enhalus* and *Thalassia*, all widely different from one another; and to

(2) 5 genera of *Potamogetonaceae*—viz.: *Cymodocea*, *Diplanthera*, *Posidonia*, *Zostera*, and *Phyllospadix*. The two first and the two last respectively are closely related to each other. Thus it might be possible to classify these 5 genera also into three groups, each group widely differing from the others.

The systematic position of the sea-grasses, their aquatic habitat, and the great structural differences between the genera, all point to their great phylogenetic age.

The natural agent of dispersal of the sea-grasses is the sea currents, as the fruits in no case ripen above the water. The *Potamogetonaceae* have droupe-like fruits, the epicarp of which is a rather thin, fleshy cover of inconspicuous colour. The *Hydrocharitaceae* have a berry, also of inconspicuous colour, containing either many small seeds (*Halophila*), or a few large ones (*Enhalus* and *Thalassia*). In *Zostera* (of the Potamogetonaceae) the epicarp, but in *Enhalus* and *Thalassia* the whole pericarp splits open, and in all the genera the "stones," or seeds, then drop out. As the fruits or seeds of the sea-grasses do not possess a floating apparatus, they are always heavier than water, and consequently the migration of the species must be very slow.

Besides this transportation by means of currents, it is possible —but not very probable—that certain fishes, and sea-mammals, such as the Dugong and Manatee, and turtles, may eat the fruits and thereby contribute to their distribution.

The dispersal by means of detached shoots, which float in the water, is almost negligible, as they do not live long when floating.

Being green autotrophous plants, the sea-grasses can grow only in shallow water where the light is sufficient for assimilation —*i.e.*, they grow only along the coasts. The depth at which they grow varies in the different species and in different seas. In northern seas (*e.g.*, *Danish*), the deeper limits of *Zostera* lie at about 10 meters. In the Mediterranean, *Posidonia* grows at greater depths, though I cannot accept without further evidence the record of its occurrence at a depth of about 50 meters.

The slow manner of dispersal and the necessity of shallow water are factors which restrict the area of occurrence of the sea-grasses.

Of the 8 genera mentioned above, *Enhalus* is monotypic. It occurs in the whole of the tropical Indopacific region. The *Zostera* genus consists of two or more species.

With the exception of *Phyllospadix*, a younger type derived from *Zostera*, and restricted to the northern Pacific, each genus inhabits

both the Indopacific and the Atlantic regions. And, as nearly all are tropical, sub-tropical, or warm-temperate plants (*Zostera* being the only one which reaches the cold regions), the occurrence of the same genus in both regions indicates that the genera are so old that they originated at a time when the distribution of sea and land was very different from that at present—this time being at least not later than Early Tertiary.[1] It is not probable that such heat-requiring plants could have migrated from the Indopacific, where they most probably originated, into the Atlantic, through the cold waters either around the Cape of Good Hope or Cape Horn.

Thus their distribution seems to indicate the great age of the sea-grasses, as does their low place in the natural system of the Phanerogams.

Hence it will, I think, be obvious that a detailed study of the geographical distribution, bearing in mind their systematic affinities, may possibly throw some light on the evolution of the sea-grasses, on the distribution of sea and land, and on the age of the present land-bridges or land-barriers separating the oceans.

The 8 genera of sea-grasses contain altogether only 30 species, most of them having a wide distribution, as is often the case with water plants.

It will be convenient to arrange them into several groups according to their geographical distribution, instead of treating each species separately.

I.—*Indopacific group* (7 species), *i.e.*, species which grow in the Red Sea, along the coasts of East Africa and of the East-African Isles, along the south and south-eastern coasts of Asia, in the Malay Archipelago, the islands of the Pacific, and, in some cases, also on the tropical coast of Australia.

II.—*Malayan group* (4 species), *i.e.*, species found in the Malayan region: south-eastern coast of Asia, Malay Archipelago, and the tropical coast of Australia.

III.—*East-African group* (2 species), *i.e.*, species found only in the Red Sea, along the coasts of East-Africa and of the East-African isles.

IV.—*Caribbean group* (6 species), *i.e.*, species occurring along the coasts of the islands of the Caribbean Sea, Florida, and the north-coast of South America, some extending as far as the Bermudas.

1. Some, e.g. *Posidonia*, perhaps even Upper Cretaceous.

V.—*Australian group* (5 species), *i.e.*, species found along the western and southern coasts of Australia and all round Tasmania, some extending as far as Queensland and New Zealand.

VI.—*Mediterranean group* (2 species), *i.e.*, species occurring in the Mediterranean and reaching the Atlantic coasts at the mouth of the Mediterranean.

VII.—*North-Pacific group* (2 species), *i.e.*, species occurring along the North-Pacific coasts of North America, and (one species) also along the coasts of Japan.

VIII.—*North-temperate group* (2 species), *i.e.*, species occurring in the northern (cold and temperate) parts of both the Atlantic and the Pacific oceans.

Of these eight groups, I.-IV. are *tropical*, V.-VI. *warm-temperate* (or subtropical), and VII.-VIII. *temperate*.

I. The *Indopacific group* consists of 7 species—viz.: Halophila ovalis; Enhalus acoroides; Thalassia Hemprichii; Cymodocea isoetifolia; Cymodocea rotundata; Cymodocea serrulata; Diplanthera uninervis.

Halophila ovalis has the widest area of distribution, as it reaches the western and southern coasts of Australia. Taken as a whole, the geographical area of this group is larger than that of any other (perhaps except that of *Zostera marina*). It is probable that the group represents the direct offspring of the old types of sea-grasses and that it inhabits their old area.

II. The *Malayan group* has four species, viz.: Halophila decipiens, Halophila ovata, Halophila Beccarii, Halophila spinulosa. All these species are rare, being found only in a few places, but it is probable that further search will show that they have a wider distribution, so that the group may perhaps be included in the Indopacific one.

[It is worth noting that *H. spinulosa* differs widely from all other species of *Halophila*, and is probably of great age. Being of quite characteristic habit, and also comparatively conspicuous, it is not probable that it has been overlooked on the continental coasts of the Indian Ocean, from which it has not yet been reported; it seems, in fact, to be restricted to the Malay region.]

III. The *East-African group* has only two members—viz.: Halophila stipulacea, Cymodocea ciliata. They are confined to the Red Sea and the western side of the Indian Ocean. (*C. ciliata* has been reported from Australia in error for *C. serrulata*.)

The two groups, II. and III., are naturally placed as subdivisions of group I., and represent two lines of differentiation from the main body of species, with its wider distribution. They show species, which have not yet attained their limits of distribution, as it seems hard to understand that a species distributed along the shores of the Red Sea and the western side of the Indian Ocean, should not be able to live along the Asiatic and Malay coasts, and *vice versa*. The absence of *Halophila spinulosa* from the Indian Ocean, and that of *H. stipulacea* and *Cymodocea ciliata* from the Malay Archipelago, are further indicative of the slow rate of migration of the sea-grasses. These well characterised species must have existed as such for a long time, probably as long as a connection between the Indian and the Pacific oceans existed.

IV. *The Caribbean group.*

Halophila Aschersonii.
Halophila Engelmanii.
Halophila Baillonis.
Cymodocea manatorum.
Diplanthera Wrightii.
Thalassia testudinum.

This group contains 4 genera with 6 species. Four of these (one of each genus—are so nearly related to 4 species of the Indopacific group, that—at least, in some cases—the characters distinguishing them from one another are quite slight.

The 4 pairs of species are the following:—

Indopacific:
Halophila decipiens.
Thalassia Hemprichii.
Cymodocea isoetifolia.
Diplanthera uninervis
Caribbean:
Halophila Baillonis.
Thalassia testudinum.
Cymodocea manatorum.
Diplanthera Wrightii.

I think it is advisable to draw the conclusion that these 4 pairs originated from 4 parent species, which were widely distributed in the tropical seas, and that the present differentiation was subsequent to an alteration in the extension of sea and land—in other words: the Caribbean species arose in their present area from ancestors which came to the Caribbean Sea from the Indopacific

at a time when the isthmus of Panama was not finally formed. From geological evidence, it is usually agreed that the isthmus is of Tertiary age, and the differentiation of the Caribbean species is consequently more recent. The close resemblance of each species to an Indopacific one agrees very well with this supposition. Their restricted geographical areas may be similarly explained.

Two of them have reached the Bermudas, and this migration accords with the direction of the Gulf Stream drift, which has a very strong flow from the coast of Florida towards the north-west, washing on its way the shores of the Bermudas. With this exception, none of the Caribbean species has yet become distributed in the Atlantic outside the Caribbean region. Although it may be admitted that our knowledge of the sea-coast flora of South America is imperfect, it is hardly likely that any rich sea-grass vegetation, if existing, could have remained unreported.[1]

Besides the 4 Caribbean species having their Indopacific partners, two species of *Halophila* also occur in the Caribbean region, one in the northern part (Florida and Bahamas), and the other in the southern parts (Antilles to Pernambuco). They are very closely allied, and must have come from a common ancestor. On the other hand, they are quite distinct from other species of *Halophila*, and no allied species has yet been found in the Indopacific region. It is possible that such a form may yet be found, but it is also possible that it has had its day and then died out there, and that the Caribbean forms are the only remnants now existing of this particular section of the genus.

V. *The Australian group.* I have referred 5 species to this group, but it is not so homogeneous as I could wish:

Cymodocea antarctica.

Posidonia australis.

Zostera capricorni.

Zostera Muelleri.

Zostera tasmanica.

The systematic value of the three species of *Zostera* is somewhat uncertain. It is possible that they ought to be reduced to two, and even one of these might perhaps be united with *Z. nana*. Their area of occurrence is along the east coast of Australia, from Cape York southwards to Tasmania, and along the eastern part of the

1. Amongst the sea-grasses on record from the African side of the Atlantic, there is a sterile species of *Diplanthera*, found at Loanda (Guinea). Whether it is the Caribbean *D. Wrightii* or, more probably, the Indopacific *D. uninervis*, already recorded from the East coast of Africa, it is impossible to say.

south coast (how far westwards I do not know); also in New Zealand and in one place on the coast of Chili. Thus the area covers the temperate part of the South-Pacific, with an outpost in the Tropics at Cape York.

The discussion of the origin of this part of the Australian group will be postponed and taken together with that of other species of *Zostera*.

The other section of the Australian group consists of two species. The first—*Cymodocea antarctica*—stands somewhat isolated within the genus. It is quite different from its nearest ally, the East-African *C. ciliata*, and it must be supposed to be an old species. The other—*Posidonia australis*—has only one congeneric species, *P. oceanica*, of the Mediterranean. Thus, these two species, which make up the isolated genus *Posidonia*, inhabit widely separated and comparatively small areas of a warm-temperate character.

The species are quite distinguishable from one another, in good agreement with their remote areas of occurrence.

The marked specific differences, as well as the isolated place of the genus within the Potamogetonaceæ, indicate their great age. The following more detailed explanation of their distribution is only a working hypothesis. In former times the genus inhabited a continuous area, of which the present two isolated areas are the only remnants. It seems as if the genus is now no longer fit for true tropical conditions, while the ancestors of the present species did occur in the Tropics. Tropical conditions, then, have driven *Posidonia* towards the north and south; and the Australian south-coast and the Mediterranean are the last refuge for a dying genus, which, to judge from identifications of leaves from Tertiary and Cretaceous times, is one of the oldest flowering plants.

VI. *The Mediterranean group* contains only two species—viz.:

Cymodocea nodosa.
Posidonia oceanica.

The two species, *Zostera marina* and *Z. nana* also occur in the Mediterranean, but are not restricted to it.

We have already dealt with *Posidonia oceanica*, when treating of the Australian *P. australis*. Neither *Posidonia* nor *Cymodocea* goes into the Black Sea, probably because its waters are neither warm nor saline enough; *Zostera marina* and *Z. nana*, on the other hand, having greater ability of adaptation, penetrate into the Black Sea.

Posidonia and *Cymodocea* have migrated through the Straits of Gibraltar out along the nearest Atlantic coast, *Posidonia* going northwards along the Iberian peninsula as far as the head of the Bay of Biscay, and *Cymodocea* northwards to Cadiz and southwards along the African coast to Senegambia and the Canaries. These interesting extensions of distribution are slight, and the two species are essentially Mediterranean in type.

As explained above, *Posidonia* has its only allied species in Australian waters. *Cymodocea nodosa* is nearest allied to *C. rotundata*, one of the Indopacific species. Therefore it seems justifiable to consider the Mediterranean species as derived from the Indopacific one; or, perhaps more correctly, to derive both from an Indopacific ancestor. The main point, however, is that both *Posidonia* and *Cymodocea* must be supposed to have come to the Mediterranean from the Indopacific region, and that this happened at a comparative early time, since the two Mediterranean species have developed so far along their own line of evolution, and are now specifically well characterised.

On the other hand, *Zostera marina* and *Z. nana* came into the Mediterranean from the north and west, through the Straits of Gibraltar.

VII. *The North-Pacific group* consists of the genus *Phyllospadix*, with its two very closely allied species—viz.: *Phyllospadix Scouleri* and *P. Torreyi*.

The genus *Phyllospadix* has arisen from *Zostera*. It differs in being dioecious and having a short, contracted rhizome (not the long, straggling rhizome of *Zostera*). The two species are so close together, that an American botanist, W. K. *Dudley*, who has studied them in situ, doubts if they are really distinct. The one (*P. Scouleri*) is very variable, while the other (*P. Torreyi*) is not, and the amplitude of the variation of the first species includes that of the second one. Both species inhabit the same part of the west coast of North America, from southern California to British Columbia; and the variable (probably older) species occurs in Japan, also making it probable that it, too, may be found in the intermediate region, along the shores of the Aleutian islands and the south coast of Alaska.

The genus being restricted to the northern Pacific, and derived from *Zostera*, has probably originated not in the tropics, but in its present home, and at a comparatively late time.

Phyllospadix serrulatus Rupr., of doubtful standing, came from Alaska.

VIII. *The North-Temperate group:*
Zostera marina and Zostera nana.

This group has really only one typical representative—viz.: *Z. marina*, but the other wide-spread species, *Z. nana*, comes perhaps also best in here, as an irregular member. Its distribution, together with that of the Australian *Zosteras*, gives, I think, the key to the evolution of the genus.

Zostera is a very much reduced type, which is supposed to have come from *Potamogeton*- and *Ruppia*-like ancestors. The flowering axis bears flowers on one side only, and the flowers are naked; but on the outer side of each flower we find a scale—the so-called *retinaculum*. This scale is sometimes supposed to be a reduced perianth. It is present in *Zostera nana*, and apparently also in the Australian species, while wanting—ordinarily—in *Z. marina*. Its presence in *Z. nana*, and allied species, seems to indicate that they are the older types, and *Z. marina* the younger. The distribution of *Z. nana* and of its allies strengthens this view. *Z. nana* is known along the coasts of Europe, from Southern Scandinavia southwards into the Mediterranean, where it penetrates into the Black Sea; further, it is found on the Atlantic coast of Morocco and in the Canaries. It does not occur along the tropical west-coast of Africa, but re-appears in South Africa and in Madagascar. It is reported with doubt from the Seychelles also. Lastly, we have records of it from Tonkin and Japan. Now it must be admitted that the identity of the plants from all these regions is not certain, as it is known, with flowers and fruits, from Europe only, and the vegetative organs show no specific distinctions.

Owing to the uncertainty of some of the records, I find it better to err on the side of caution, and to make the more general statement:—that a narrow-leaved and small *Zostera* has been found in the above-mentioned areas. I would associate with this form the closely-allied three Australian species, the distribution of which I have already given. In this way we get one group of narrow-leaved and small Zosteras, with an almost word-wide distribution. It is worth noting that this group is absent from both coasts of North America, and that the records are very scanty as regards tropical localities. The distribution has some resemblance to that of the genus *Posidonia*, but it is less restricted. And I think the same explanation holds good here—viz.: the Zostera group originated in the Tropics, and migrated both northwards and southwards, nearly disappearing in its original home. Mean-

while the extinction in the Tropics of *Zostera* has not been as complete, as is the case with Posidonia; and *Zostera* does not show such marked signs of waning as it does.

The younger type of the genus, *Z. marina*, is distributed along the coasts of Europe, from the Black Sea and the Mediterranean in the south to Lapland (Murman coast) in the north. From the British Isles it has reached the Faeroes and Iceland; and it is also found at one locality on the western side of Greenland. But its occurrence here is, I think, due to accidental transport by man, as it is near places inhabited, onwards to the present time, from the time of the old Norse colonists.[1] Along the Atlantic coast of America we find *Z. marina*, extending from the Gulf of St. Lawrence to Virginia. Quite separated from its Atlantic area is the North Pacific one, which on the American side extends from Southern California to Alaska, while the Asiatic side includes the coasts of Manchuria and Japan.

Z. marina is thus distributed along all the coasts of the North Atlantic and the North Pacific, but it is wanting in the intermediate area, the Arctic Ocean (with the above-mentioned exception of Greenland). The question now naturally arises: How has it come to have this discontinuous distribution? The possibility that it originated during a warmer climate in the Arctic sea, and was driven southwards by a deterioration of the climate, is hardly probable.

The origin of the genus was supposed to be tropical, and it is more probable than *Z. marina* also, which is by no means young, in spite of being younger than the *Z. nana* group, originated in a warm ocean and migrated northwards; but the evidence is not sufficiently clear whether this home was the Pacific or the Atlantic. As it is not probable that the one species originated in both oceans, a migration from one ocean to the other seems necessary. We have then two ways of migration: (1) Either it migrated through a sea-connection which does not now exist—*e.g.*, through the Caribbean connection (just as it is probable that the Caribbean group of sea-grasses did); (2) or, it migrated by way of the Arctic ocean at a time when its waters were warm. The latter way of migration seems more probable from a biological point of view, and is better in accord with the present-day conditions life of the species.

Much of what has ben said here about the evolution of the sea-grasses and their migrations is, of course, only hypothetical, and

may be wrong. Still, it seems to me that the existing facts of the distribution of the genera and species make deductions of that kind allowable. They are a help in gaining an idea of how these interesting remnants of the older types of Flowering Plants attained their present areas of distribution.

The peculiarities of distribution of the sea-grasses are not without parallel. Amongst the Marine Algae similar cases have been reported. *George Murray* (1873) has pointed out that there is a great resemblance between the algal flora of the Caribbean Sea and that of the Indopacific region. He supposes it to be explicable by a migration by way of the Cape. *N. Svedelius* (1906) agrees with Murray as to the great resemblance of the floras, which he has himself studied, especially in *Caulerpa* (surely a very old type); but his explanation necessitates a water-connection where the Isthmus of Panama now is. This is essentially the same explanation as that I have offered with regard to the origin of the Caribbean sea-grasses.

III. Summary.

1. The Marine Flowering plants, the *sea-grasses*, belong to two families of the old monocotyledonous cohort, the *Helobieae*. They are reduced and specially adapted ancient types.

2. With one exception (the monotypic *Enhalus*), the genera all occur in the Indopacific and the Atlantic regions. This distribution indicates that the origin of the genera goes back to a time when the relation of sea and land was different from that now—viz. to the earlier part of the Tertiary period.

3. The dispersal of the sea-grasses is restricted and slow. It is mainly due to sea-currents, but the seeds are not able to float, and detached pieces of rhizomes do not live long.

4. The 8 genera contain altogether only 30 species, which can be arranged into 8 groups, according to their geographical distribution—viz.: (a) 4 *Tropical:* Indopacific, Malayan, East-African and Caribbean; (b) 2 *Warm-temperate* (or sub-tropical): Australian, Mediterranean; and (c) 2 *Temperate:* North-Pacific and North-Temperate..

5. The Indopacific group contains the majority of the species, especially when we include the Malayan and East-African groups as sub-divisions (13 species). The parent home of the sea-grasses lies within the geographical area of this group.

6. The Caribbean group (6 species) has 4 species, each of which is closely allied to an Indopacific one, and it is probable that the

whole group migrated from the Indopacific to the Caribbean Sea at a time when there was a connection between them through the Isthmus of Panama. Two of these species have reached the Bermudas, but elsewhere they are not found outside the Caribbean region, the Atlantic Ocean being very poor in sea-grasses.

7. The genus *Posidonia* has at the present time one species along the south coast of Australia, and the other in the Mediterranean. It is supposed that they represent the last remnants of a genus whose home was somewhere in the Indian region, and that it was driven away towards the north and the south.

8. The other species of the Mediterranean group, *Cymodocea nodosa*, also migrated from the south-east into the Mediterranean, while the two Zosteras of this sea came from the north.

9. The genus *Phyllospadix* is restricted to the North Pacific. Its morphological characters indicate its derivation from Zostera.

10. The narrow-leaved, small *Zosteras* (*Z. nana*, and the three Australian species) are supposed to be the older type of the genus, as they still have the "retinaculum" (the scale attached to the flower). When taken together, their distribution is "bipolar," with a few outposts in the Tropics.

11. It is supposed that the genus *Zostera* originated in a warm sea and migrated towards the north and the south.

12. The younger type, *Zostera marina*, is yet an old species. It is supposed that it also originated in a warm sea (perhaps in the Indopacific region), wandered northwards, and in one manner or another came from the Pacific into the Atlantic, or *vice versa*.

13. With the exception of *Phyllospadix*, which originated in the North-Pacific, and arose from *Zostera*, all the genera of sea-grasses are supposed to have arisen in the Tropics, where the home of most of them still is, *Zostera marina* being the only species which extends into the Arctic Sea.

14. The distribution of the species still requires investigation. This applies especially to the three Australian *Zosteras*, which are little known, both systematically and geographically.